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Pierre Moret. Altitudinal distribution, diversity and endemism of Carabidae (Coleoptera) in the páramos of Ecuadorian Andes. *Annales de la Société Entomologique de France*, 2009, 45 (4), p. 500-510. hal-00723855

HAL Id: hal-00723855

<https://hal.science/hal-00723855>

Submitted on 14 Aug 2012

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Altitudinal distribution, diversity and endemism of Carabidae (Coleoptera) in the páramos of Ecuadorian Andes

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Abstract. Species richness and diversity of Carabidae (Coleoptera), as well as rates of endemism, are studied along altitudinal transects in the páramo of Ecuadorian Andes, from 3500 to 5000 m. Whereas a global tendency to reduction of species richness is evident from 4200 m upwards, two zones of high diversity and high proportion of endemic species occur at 3800–4000 m and at 4200–4400 m. Species turnover between grass páramo and superpáramo is significantly higher in drier mountains, especially in the Western Cordillera, than in humid mountains of the Eastern Cordillera. The altitudinal range of Carabid species tends globally to decrease along the vertical gradient, but with important local variations due to microenvironmental factors, especially humidity rate. When compared with recent phytogeographical studies, these results tend to support the idea that the majority of tussock-grass páramo is a secondary anthropogenic ecosystem. On the contrary, it is argued that the xeric landscape of the Chimborazo “arenal” is primordial, based on the presence of a stenotopic and possibly relict species, *Pelmatellus andium* Bates 1891.

Résumé. Distribution en altitude, diversité et endémisme des Carabidae (Coleoptera) dans les páramos des Andes Equadorienne. La diversité et le taux d'endémisme des Carabidae (Coleoptera) sont analysés sur plusieurs transects altitudinaux dans les páramos des Andes de l'Equateur, entre 3500 et 5000 m. Alors qu'une tendance générale à la diminution du nombre d'espèces apparaît à partir de 4200 m, deux zones de plus grande diversité et à fort taux d'espèces endémiques ont été mises en évidence à 3800–4000 m et à 4200–4400 m. Le taux de remplacement des espèces entre le páramo herbacé et le superpáramo est nettement plus élevé dans les massifs les plus secs, en particulier dans la Cordillère Occidentale, que dans les massifs humides de la Cordillère Orientale. L'amplitude altitudinale des espèces tend globalement à diminuer avec l'altitude, mais on note d'importantes variations d'une montagne à l'autre ou d'un versant à l'autre, en raison des conditions du milieu (en particulier le degré d'humidité). À partir d'une comparaison avec des études phytogéographiques récentes, on apporte des arguments à l'hypothèse selon laquelle la plus grande partie du páramo herbacé est une formation secondaire d'origine anthropique. À l'inverse, il est suggéré que le paysage semi-désertique de l'“arenal” du Chimborazo est climacique, compte tenu de la présence d'une espèce sténopéc et vraisemblablement relicte, *Pelmatellus andium* Bates 1891.

Keywords: Páramo, Carabidae, Ecology, Biodiversity, Endemism.

Páramo is a tropical alpine ecosystem that ranges in the Andes from northern Peru to the Cordillera de Talamanca in Costa Rica, above continuous forest line (3400–3600 m) and below permanent snowline (4800–5000 m), with particular features such as: low ambient temperatures, higher daily oscillations than seasonal ones, and a high frequency of night frost throughout the year. It is formed by tussock grasses, cushion plants, and sclerophyllous shrubs.

Following its vegetation structure, the páramo has been divided into three altitudinal belts: the subpáramo, which is a transitional zone with the

montane forest, the grass páramo, and the superpáramo (van der Hammen & Cleef 1986; Luteyn 1999; for Ecuador: Acosta-Solís 1984; Sklenár & Ramsay 2001). Grass páramos occur in Ecuador from about 3400 to over 4000 m. This formation is dominated by bunch- or tussock-forming grasses. In between the grass tussocks grow a diverse assemblage of herbaceous plants, scattered small shrubs and cushion plants. Most grass páramos are burned annually or every few years, presenting therefore morphological and physiological adaptations to survive frequent fires (Lægaard 1992). The superpáramo usually occurs between 4100–4200 m and 4800–4900 m and is subdivided into two belts, the lower and upper superpáramo (Sklenár & Balslev 2005). Lower superpáramo (4100–4200 to 4400–4500 m) is usually richer in species, with sclerophyllous shrubs and cushion plants, but

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Accepté le 2 mars 2009

tussock grasses are usually also important. The upper superpáramo (above 4400–4500 m) is characterised by shortstem grasses, prostrate subshrubs and herbs, acaulescent rosettes and cushion plants. The vegetation is poor and patchy, being confined to a few favourable habitats.

Most of the studies that have been dedicated to the ecology and the biogeography of the páramo deal with plants or vertebrates. Carabid beetles are rarely taken into account in such works, except in local ecological surveys of single mountains (Perrault 1994; Sturm 1994; Moret 2001; Smithers & Atkins 2001; Camero 2003) or in physiological researches (Sømme *et al.* 1996). Nonetheless, Carabidae have proved to be very useful for ecological studies, inasmuch as many of them are stenotopic and linked to specific niches (Thiele 1977; Desender *et al.* 1994; Dajoz 2002). Moreover, in high altitude communities, their high rate of endemism provides valuable data for biogeographic analyses (Noonan *et al.* 1992; Liebherr 1994).

In a recent revision of the Carabidae that live in Ecuadorian páramos above 3400 m (Moret 2005), 204 species were treated and arranged in 16 genera and 8 tribes (table 1). Most of them (94 %) are micropterous, with a very low dispersal power due to the loss of functional metathoracic wings, and are therefore restricted to small montane areas. This paper deals with some of the ecological and biogeographical results of that study, as far as species richness, diversity and endemism are concerned. It will address the

following questions: How do species richness and beta-diversity vary along altitudinal gradients? How are microendemic species distributed along these gradients? A comparison will also be drawn with the results of recent phytogeographic studies (Lauer *et al.* 2003; Sklenár & Lægaard 2003; Sklenár & Balslev 2005; Sklenár 2006), in order to contribute to a better definition of altitudinal zonation and areas of endemism within Ecuadorian páramos.

Material and methods

Our taxonomic treatment of the páramo Carabids of Ecuador was based on direct examination of *ca* 8500 specimens found throughout that country above 3400 m. 2481 specimens were collected by the author during several field work periods (1984–1986, July–August 1988, April 1991, January 1995, July–August 1998, July 2001), the rest by 31 collectors or teams of collectors between 1853 and 2002. A detailed checklist of materials can be found in Moret 2005: 21–24 (see also below in the acknowledgment section). A few minor changes were introduced in this data set, following recent revisions of the genera *Bembidion* (Toledano 2008) and *Oxytrechus* (Allegro *et al.* 2008).

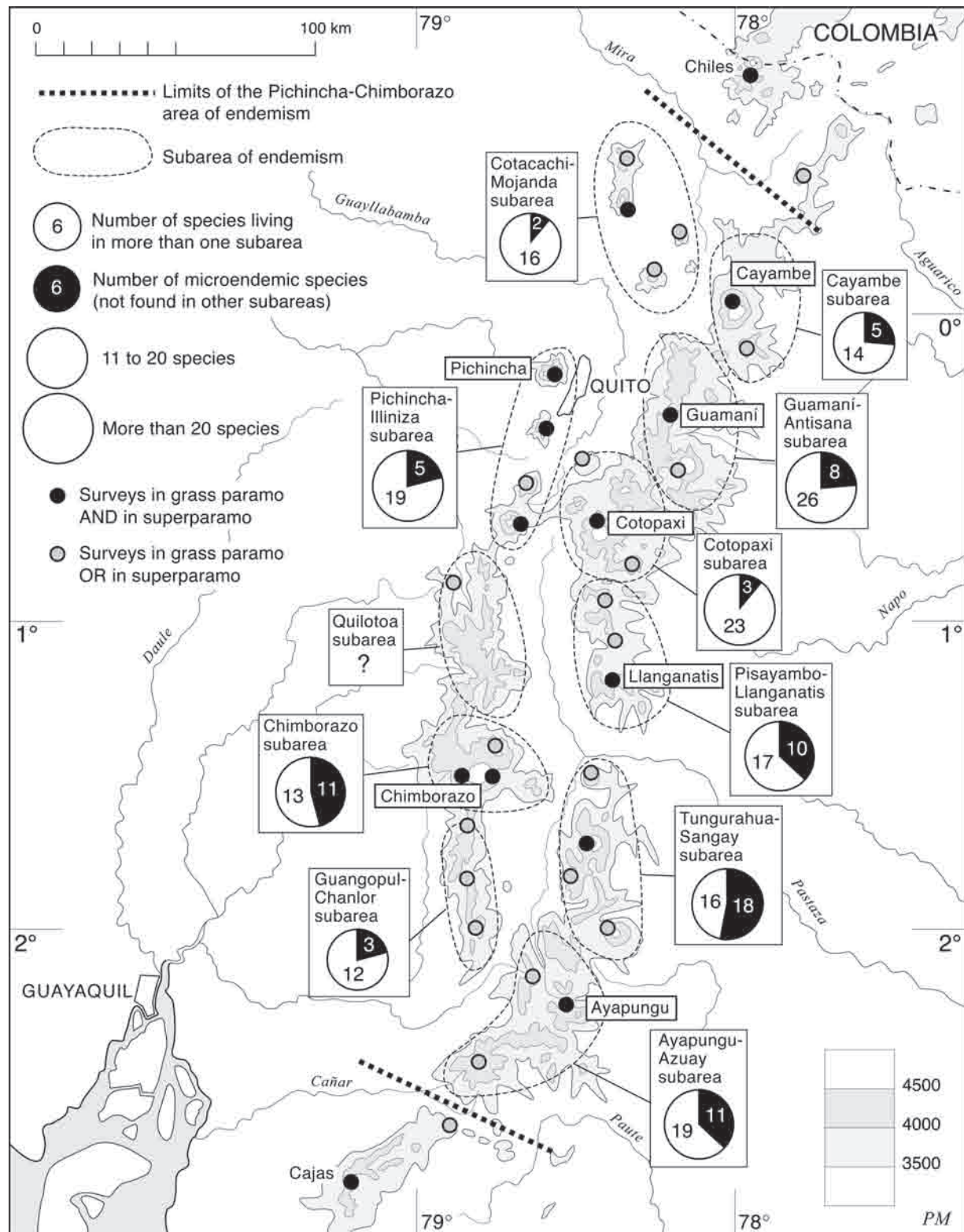
As the first level of analysis, all specimens bearing precise altitudinal data (*ca* 7500) were taken into account as a means to highlight global tendencies at generic level. But this general data set is far too heterogeneous to support accurate ecological and biogeographical analyses, since it sums materials collected by different researchers or travellers, each with distinct purposes and using different techniques.

Thus, at a second stage, in order to allow more precise faunistic assumptions, the focus was restricted to the Pichincha-Chimborazo area of endemism, which has been far better

Table 1. Genera of Carabidae found in Ecuadorian páramos above 3400/3500 m.

Am. = American; S.Am. = South American; M./S.Am. = Middle and South American.

Tribe	Genus	Described species in Ecuador	Biogeographic area	Maximum elevation in Ecuador
Migadopini	<i>Aquilex</i> Moret 1989	1	High-andean endemic	4300
Trechini	<i>Trechisibus</i> Motschulsky 1862	3	Austral Am.	4800
	<i>Oxytrechus</i> Jeannel 1927	12	Tropical andine	3800
	<i>Paratrechus</i> Jeannel 1920	16	Montane M./S.Am.	4600
Bembidiini	<i>Ecuadion</i> Moret & Toledano 2002	30	Montane M./S.Am.	5070
Harpalini	<i>Notiobia</i> Perty 1830	2	Temperate Am.	3850
	<i>Bradycellus</i> Erichson 1837	2	Temperate Am.	3800
	<i>Pelmatellus</i> Bates 1882	12	Montane M./S.Am.	4800
Pterostichini	<i>Blennidus</i> Motschulsky 1865	24	Tropical andine	4900
Platynini	<i>Incagonum</i> Liebherr 1994	2	Temperate S.Am.	3800
	<i>Sericoda</i> Kirby 1837	1	Holarctic	4000
	<i>Glyptolenoides</i> Perrault 1991	2	Tropical andine	3900
	<i>Dyscolus</i> Dejean 1831	89	Neotropical	4970
Dercylini	<i>Dercylus</i> Castelnau 1832	5	Neotropical	4200
Lebiini	<i>Mimodromius</i> Chaudoir 1873	2	Temperate S.Am.	4000
	<i>Lebia</i> Latreille 1802	1	Pantropical	3850

**Figure 1**

Map of the páramos in the central and northern Andes of Ecuador, with the limits of the Pichincha-Chimborazo area of endemism and of its subareas (modified from Moret 2005).

Table 2. Characteristics of eight selected altitudinal transects, between 3500 and 5000 m elevation, in seven mountains of the Pichincha-Chimborazo area of endemism.

	Province	Coordinates	Maximum elevation	Climate	Total Nr of species	Micro-endemic species
Pichincha East and South slopes	Pichincha	0°10'S 78°35'W	4794	Medium	18	3
Chimborazo West slope	Chimborazo	1°28'S 78°52'W	6310	Dry	21	6
Chimborazo East slope	Chimborazo	1°28'S 78°46'W	6310	Humid	17	8
Cotopaxi North slope	Cotopaxi	0°40'S 78°26'W	5897	Dry	29	2
Cayambe West and North slopes	Pichincha	0°02'N 77°59'W	5790	Humid	20	4
Guamaní East slope	Napo	0°18'S 78°14'W	4490	Wet	28	8
Llanganatis North slope	Tungurahua	1°10'S 78°20'W	4390	Humid	20	8
Ayapungu West slope	Chimborazo	2°17'S 78°35'W	4730	Humid	27	9

surveyed than the others (fig. 1). In that particular area, the faunistic analysis was limited to 142 species that are true páramo dwellers. Four species that have been registered sporadically at low elevations in the grass páramo were excluded, because they belong predominantly to the upper montane forest fauna: *Bembidion (Ecuadion) sanctaemarthae* Darlington 1934 (= *Bembidion (Ecuadion) giselae* Moret & Toledano 2002), *Glyptolenoides azureus* (Chaudoir 1859), *Incagonum aeneum* (Reiche 1843), and *Dyscolus bordoni* Moret 1993. Three more taxa were dismissed because they are highly specialised azonal species: *Sericoda bembidioides* Kirby 1837 (a widespread pyrophilous insect), *Lebia paramicola* Moret 2005 and *Mimodromius leleupi* Mateu 1970 (two ectoparasitic species).

Finally, special attention has been paid to seven mountains of the Pichincha-Chimborazo area, where complete or almost complete altitudinal transects can be reconstructed along one or several slopes, from the bottom of the grass páramo up to the top of the superpáramo (table 2). Based on these data, altitudinal variation of Carabid diversity was studied between 3500 and 5000 m to test possible occurrences of faunistic zonation, especially between grass páramo and superpáramo (fig. 4).

The altitudinal range of the species was calculated as the

difference between the lowest and highest place where they were collected. Altitudinal data given by the labels of individual specimens were used to work out the number of species collected in any vertical interval of 100 m, as a means to measure species richness per altitude. The following analyses are therefore mostly based on presence-absence data. The lack of long-lasting and systematically planned samples throughout entire vertical transects makes impossible any attempt to measure species abundance with greater precision.

The possibility of quantifying species diversity in vertical transects is hindered too by the heterogeneity of the data set. To compare as a whole the grass páramo Carabid community with that of the superpáramo, as we tried it in a previous work (Moret 2005: tab. 35), is almost impossible, insofar as the definition of these communities is biased by subjective assumptions, due to altitudinal variations of the limit between both floristic belts and to the existence of a transition zone where different faunistic elements overlap. Here we preferred to compare the composition of Carabid communities at four intervals of altitude that were arbitrarily selected: 3600–3700, 3900–4000, 4200–4300 and 4500–4600 m (tab. 3). Species diversity was calculated using the Sørensen similarity index: $2A / (a_1 + a_2)$, where a_1 refers to species scores in the sample 1,

Table 3. Diversity of Carabid species at different elevations on seven altitudinal transects. Columns 2, 4, 6, 8: number of species. Columns 3, 5, 7 (S.I.): Sørensen similarity index.

	3600–3700 m	S.I.	3900–4000 m	S.I.	4200–4300 m	S.I.	4500–4600 m
Pichincha	7	0,71	7	0,27	8	0,75	8
West Chimborazo	11	0,64	11	0,25	5	0,50	3
Cotopaxi	12	0,50	8	0,25	8	0,46	5
Cayambe	8	0,27	7	0,61	6	0,61	7
Guamaní	7	0,44	20	0,44	12		-
Llanganatis	10	0,47	7	0,37	9		-
Ayapungu	11	0,33	7	0,59	10		-

a, to species scores in the sample 2, and A to scores of species shared between both samples (Koleff 2005).

Definition of endemic and microendemic species, as well as areas of endemism, are the result of a previous work (Moret 2005: 262). Based on the distribution patterns of 191 micropterous species (which amount to 94 % of all páramo Carabid species), five areas of endemism were distinguished, from north to south: the Carchi area, the Pichincha-Chimborazo area, the Cajas area, the Saraguro area, and the Loja area. These results are strongly supported by a very high rate of precinctive species (*i.e.*, species that have not been found in any other area): 85.7 % in Carchi, 94.5 % in Pichincha-Chimborazo, 81.4 % in Cajas, 80 % in Saraguro and 100 % in Loja. On a smaller scale within the Pichincha-Chimborazo area (fig. 1), the distributional patterns of microendemic species (*i.e.*, species restricted to areas less than 1000 km²) enabled us to define 13 subareas of endemism, where the percentage of precinctive species is 10 % or more.

Results

Genus diversity

With only 16 taxa (table 1 and fig. 2), generic richness is low in the Ecuadorian páramo when compared with other neotropical ecosystems. In the nearby Andean montane forest, the number of known genera of Carabidae ranges far above 50 (unpublished data). The number of genera is the highest in the basal zone of the páramo, due to the presence of several genera composed of sylvatic or ruderal species that occasionally enter the grass páramo at low altitudes: *Incagonum*, *Glyptolenoides*, *Notiobia*, *Sericoda*. 14 genera are recorded from altitudes around 3500–3600 m, whilst from 4100 m upwards only 9 genera are found. The fauna of the upper superpáramo, above 4400 m, is restricted to 6 genera (*Bembidion*, *Oxytrechus*, *Paratrechus*, *Dyscolus*, *Blennidus* and *Pelmatellus*), represented there by specialised orobiont forms. In global terms, these six genera are clearly dominant in Ecuadorian páramos (fig. 2). Their curves reveal an optimum of species richness at middle elevations (from 3800 to 4100 m), and only then a progressive diminution. Only one genus, *Aquilex*, is endemic to Ecuadorian high Andes and can be considered as an exclusive páramo specialist. The other genera are all represented in the upper montane forest by species that are adapted to leaf-litter or arboreal habitats.

Species richness varies greatly from one genus to the other, with *Dyscolus* containing 44 % of all species. *Dyscolus* species show a great variety of adaptations to almost every ecological condition that can be found in páramos, from the xeric puna-like “arenal” to the uppermost superpáramo. Other genera are linked with narrower habitat conditions. *Aquilex*, *Paratrechus* and part of *Bembidion* are riparian or highly hygrophile; *Blennidus* and *Pelmatellus* contain a majority of generalist species, along with a few xerophile species.

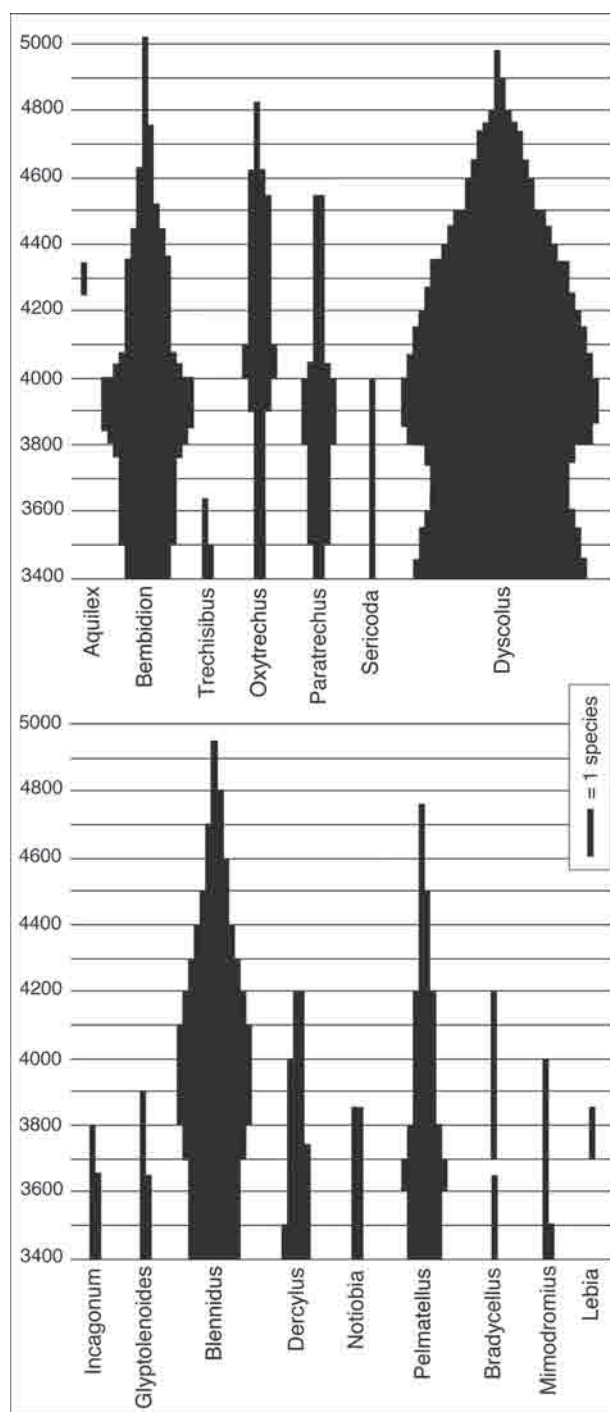


Figure 2

Altitudinal range and species richness of the 16 Carabid genera that live in Ecuadorian páramos (global data). In each 100 m-interval, the number of black vertical bars indicates the number of registered species.

Species diversity and altitudinal distribution

It is generally assumed that in montane faunas, diversity gradually decreases as altitude increases (Stevens 1992). The case of páramo Carabids is not so straightforward. Whereas a global tendency to reduction of species richness is evident from 4200 m upwards, a completely different situation is observed in the grass páramo between 3400 and 4200 m (fig. 3). In that particular floristic belt, species richness reaches higher scores at medium elevations than at low ones, with a major peak of diversity at 3800–4000 m, as proved by a conspicuous rise of the number of microendemic species. Even in the superpáramo, a minor peak can be detected between 4200 and 4400 m, being characterised by a pause in the decrease of the non-endemic species and a slight recovery of the microendemic ones.

The analysis of individual transects allows a better understanding of these phenomena (fig. 4 and table 3). Two major patterns can be distinguished. A first group of mountains includes Pichincha, West Chimborazo and Cotopaxi, with four characteristics: 1. high or

moderately high similarity within the grass páramo, from 3500 to 4000 m; 2. important turnover of species between grass páramo and superpáramo, as indicated by a very low similarity index (*ca* 0,25) between the 3900–4000 and 4200–4300 m intervals; 3. reduced turnover within the superpáramo; 4. highest species richness around 4000–4200 m in normal conditions (Pichincha). On Cotopaxi and on the West slope of Chimborazo, a sudden collapse of the species richness at the same elevation is due to local factors: arid microclimate and/or recent volcanic activity (see below).

Results of less complete surveys on the Illiniza, Atacazo and Corazón volcanoes suggest that this pattern is widespread all along the Western Cordillera in the Pichincha-Chimborazo area. The case of the Cotopaxi north transect seems to be an exception, as it belongs to the Eastern Cordillera.

A second group is formed by four mountains of the Eastern Cordillera (Cayambe, Guamaní, Llanganatis, Ayapungu), along with the Eastern slope of the Chimborazo in the Western Cordillera. They

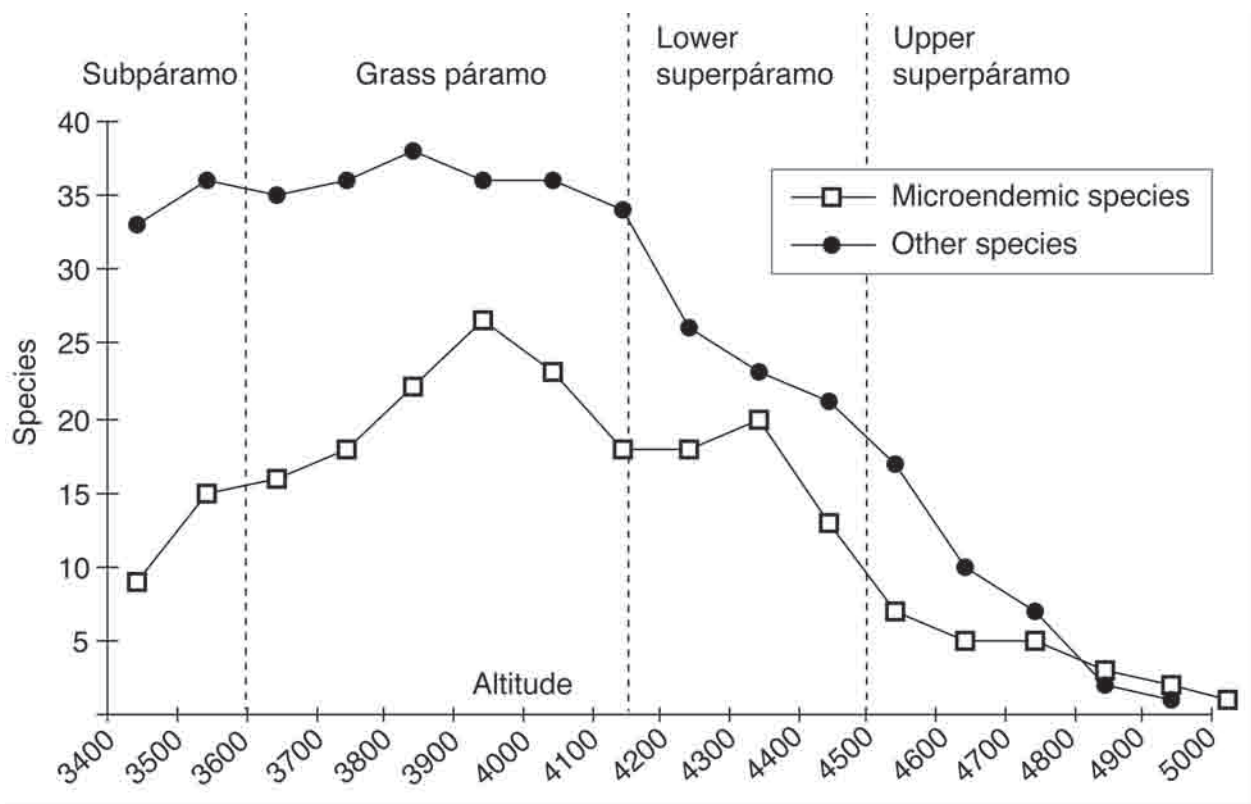
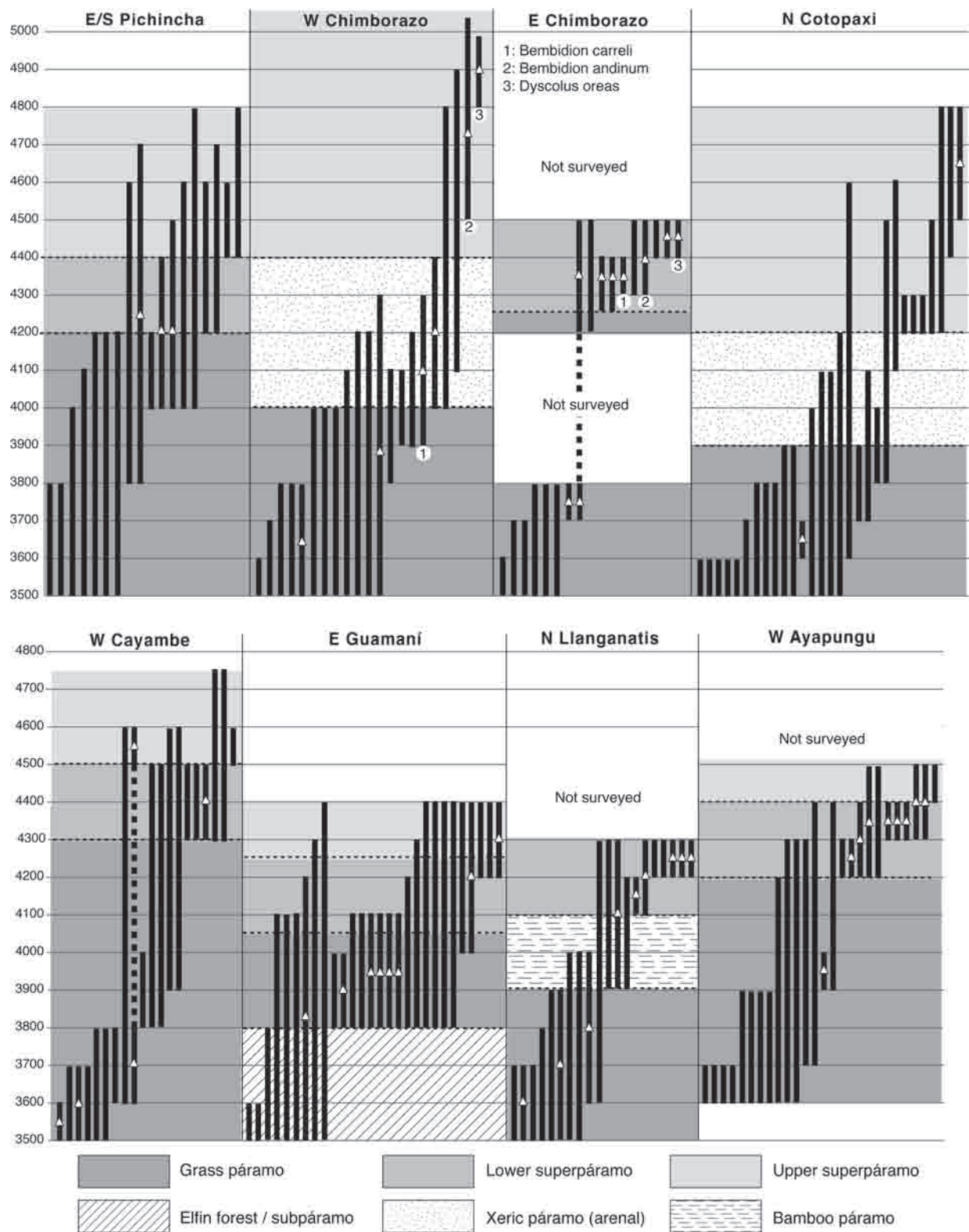


Figure 3

Altitudinal variation of species richness (per 100 metres-intervals of altitude) for 142 Carabidae species of the Pichincha-Chimborazo area of endemism. White squares: microendemic species; black circles: other species.

**Figure 4**

Altitudinal distribution of Carabid species in vertical transects of seven mountains of the Pichincha-Chimborazo area. Details about geographical situations in table 2. White triangles: microendemic species.

present three distinctive traits: 1. similarity is low or moderate between the lower and the upper part of the grass páramo, from 3500 to 4000 m; 2. carabid communities at 3900–4000 m and at 4200–4300 m are moderately similar (Cayambe, Ayapungu) or moderately dissimilar (Guamaní, Llanganatis), but in general terms, similarity index between grass páramo and superpáramo is always higher than in the first group; 3. species richness reaches very high scores in non-disturbed páramos, being extremely high from 3900 to 4100 m in the Guamaní transect (20 different species occurring in that interval), due to exceptional environmental conditions: high humidity, absence of grazing, diverse vegetation.

These global tendencies are locally modified by environmental or historical factors. Disturbances, such as volcanic activity or soil erosion, are important features in some páramos of Ecuador and may significantly alter the general altitudinal patterns (Šklenár & Balslev 2005). For example, species richness has been dramatically reduced by volcanic activity of the last two centuries on the slopes of Cotopaxi, between 3900 and 4200 m (fig. 4), and at all elevations on currently active volcanoes such as the Tungurahua or the Sangay, both in the Eastern Cordillera (Moret 2005). Regarding climatic factors, the case of the arid western side of Chimborazo will be discussed below.

Altitudinal range

Altitudinal range is quite variable among páramo Carabid species. In the genus *Dyscolus*, the mean altitudinal range is close to 500 m, but some species have been registered at almost all elevations from 3400 m up to 4400 m (Moret 2005: fig. 366). If we discard the species registered at low elevations that are known to live far below 3500 m in the subpáramo, the altitudinal range of Carabid species tends globally to decrease along the vertical gradient, i.e., the species from higher altitudes tend to have a narrower altitudinal range. This result seems to differ from floristic data in similar contexts, since botanical surveys of the Illiniza volcano, situated in the Western Cordillera south of the Pichincha, have shown that the mean altitudinal range of species per altitude increases along the gradient (Šklenár 2006).

The altitudinal range of several widespread species differs greatly from one mountain to another, or even from one slope to the other on the same mountain. These local variations may be important, as shown by a detailed analysis of the distribution of four species of the genus *Dyscolus* (Moret 2005: 246–248). In the case of *Dyscolus diopsis* (Bates 1891) and *D. megacephalus* (Bates 1891), it is quite clear that the range of these

species is broader and starts at lower elevations in humid páramos (Cayambe, Guamaní, Ayapungu), whereas it is much narrower and starts at higher elevations in drier contexts, being usually restricted to the superpáramo (Cotopaxi, Pichincha). On the West slope of Chimborazo, *Dyscolus oreas* (Bates 1891) ranges from 4800 m to 4970 m, in the uppermost portion of the superpáramo, whereas on the East slope, the same microendemic species is present as low as 4400 m (fig. 4, n° 3). A similar pattern is shown by *Bembidion andinum* Bates 1891 (n° 2), but on the contrary *Bembidion carreli* Moret & Toledano 2002 lives higher on the East slope than on the West one (n° 1). These data reveal the role played by local environmental factors on stenotopic flightless insects.

Distribution of microendemic species

If we take into account all the species of the Pichincha-Chimborazo area, the mean altitudinal range of the best known species –particularly those of the genus *Dyscolus*– appears to be much broader in the widespread species than in the microendemic ones. In other words, there is a positive correlation between restricted geographic area and narrow altitudinal distribution.

Proportion, richness and altitudinal distribution of microendemic species vary greatly from one mountain to another, and do not seem to respond to any clear general patterns. Only in some mountains of the above described second group (Eastern Cordillera + East Chimborazo), we can observe a very high proportion of microendemics in a few particular contexts: Guamaní from 3800 to 4100 m, Llanganatis above 4100 m, Ayapungu above 4200 m, East Chimborazo above 4300. Except in the particular case of Guamaní, these data point to the lower superpáramo as to a hotspot of diversity with a high proportion of microendemics.

Discussion

The main strategy of páramo insects seems to be behavioural avoidance of cold temperatures and excessive dryness (Smithers & Atkins 2001). It has been demonstrated that resistance to coldness and dessication is surprisingly low among Ecuadorian high-altitude Carabids (Sømme *et al.* 1996). Owing to the lack of physiological adaptation, these insects are in need of shelter under rocks, stones or cushion plants, or among the superficial roots of tussock-grasses, in order to avoid the extreme nycthemeral contrasts of the high Andean climate. Consequently, Carabid communities depend on vegetation structure and soil morphology as well as on the altitudinal factor itself. This is the reason

why many Carabid species have different altitudinal ranges in different mountains, or in different slopes of the same mountain, according to local climatic, pedologic and floristic conditions.

Diversity in the grass páramo

Carabid assemblages demonstrate that the highest diversity occurs in the upper part of the grass páramo (3900–4100 m) and in the lower part of the superpáramo (4100–4400 m), then falling off steeply into the upper superpáramo. In the grass páramo, species diversity is much higher at high elevations (above 3800 m) than in its lower part (fig. 3). These results contradict the usual assumption of a gradual decrease of diversity and species richness along altitudinal gradients (Stevens 1992). They can be explained at some extent by the fact that the upper limit of the species that are restricted to the grass páramo overlaps with the lower limit of the high altitude orobionts, so that the maximum diversity occurs in a transitional zone where many flightless páramo Carabid species are likely to be found. But the main cause of the relatively depauperate fauna of the grass páramo, between 3500 and 3900 m, is probably anthropogenic.

It has been assumed that the climax vegetation of the Andes was forest up to 4200–4300 m, and that present-day grass páramo is a fire-induced anthropogenic landscape (Lægård 1992). Carabid distribution and diversity allow us to contribute to this debate with five points. 1/ Species richness is frequently higher in the lower superpáramo, around 4200–4300 m, than in grazed páramos around 3700–3800 m, particularly in the Eastern Cordillera (fig. 4). 2/ There is a high faunistic similarity between forest edge communities and grass páramo communities (Moret 2005). 3/ There is a low or moderately low faunistic similarity between grazed páramo communities and superpáramo communities (table 3). Conversely, there is much less turnover between the upper part of grass páramo and the superpáramo in the few transects, such as Guamaní, where anthropic pressure is low. 4/ In the grass páramo, communities are dominated by a few generalist and eurytopic species, with broad altitudinal ranges: *Bembidion fulvocinctum* Bates 1891 and *B. cotopaxi* Moret & Toledano 2002, *Dyscolus alpinus* (Chaudoir 1878) and *D. denigratus* (Bates 1891), *Blennidus pichinchae* (Bates 1891), *Dercylus cordicollis* (Chaudoir 1883) and *Pelmatellus columbianus* (Reiche 1843). 5/ Percentage of microendemic species is lower in the grass páramo, higher in most of the superpáramos (fig. 4).

These observations indicate clearly that the Carabid communities of the grazed páramo are impoverished,

dominated by typically pioneer or opportunistic species, some of which come from the ecotone habitat of the forest edge. In that way, the results of this study strengthen the hypothesis of the tussock-grass páramo being a secondary anthropogenic ecosystem. In non-disturbed conditions, biotopes similar to the lower superpáramo may have existed locally as low as 3900 m, mixed with patches of *Polylepis* forest, as indicated by the residual presence of superpáramo specialists at elevations between 3900 and 4100 m in almost all the surveyed transects.

Only a few páramos below 4200 m can be considered to represent true climax vegetation, based on a greater species richness and higher percentage of microendemic species. On the one hand, there are the bamboo páramos of the most humid areas of the Eastern Cordillera, whose entomological fauna is still poorly known. A partial survey on the north slope of Llanganatis (table 2 and fig. 4) indicates that the Carabidae that have been found in this type of páramo are both related with the superpáramo community and with the most hygrophilic elements of the lower grass páramo community. In the Guamaní area, the outstanding richness of the Carabid community between 3800 and 4000 m is due to the great diversity of ecological niches in a patchy mosaic of shrub páramo, *Polylepis pauta* mixed woodland and swamps (Lauer *et al.* 2003: 80).

On the other hand, there is the xeromorphic páramo, locally called “arenal”, of the western side of Chimborazo. This desert-like area with very sparse and patchy vegetation, in strong contrast with the dense humid páramo of the eastern side, is the result of a rain-shadow phenomenon on the western leeward side of the mountain. A similar pattern, though less contrasted, is known on the Southwest side of the Antisana, a volcano situated halfway between Guamaní and Cotopaxi. According to Sklenár & Lægård (2003), there is a higher floristic similarity between the two western and two eastern sides of these mountains, respectively, than between the opposite sides of each mountain. Despite limited faunistic surveys on Antisana, the same conclusion can be drawn from the composition of Carabid communities. On Chimborazo, similarity is very low between the west and east slopes, though a typical xerophilic species of the Chimborazo “arenal”, *Pelmatellus andium* Bates 1891, is present also at the same elevation on the west side of the Antisana.

As to its floristic communities, the dry western Chimborazo has a low species richness and low beta-diversity; it is among the least diverse páramos in Ecuador, with 20 % less plant species than on the opposite humid east side (Sklenár & Lægård 2003).

According to these authors, the desert-like “arenal” would be an anthropogenic, depauperate landscape “due to the combined effect of (1) rain-shadow of the volcano, (2) human-induced disturbance of the vegetation by cattle-breeding and heavy grazing, and (3) resulting erosion”. This assessment is not supported by faunistic data. Species richness is relatively low in the “arenal”, but its community is quite different from that of standard grass páramo at the same elevation in other mountains of the Western Cordillera. Locally, there is a very low similarity between the “arenal” community at around 4200 m and that of the grass páramo under 4000 m (table 3). Moreover, this xerophile community includes a stenotopic element, *Pelmatellus andium* Bates 1891, which is only known from three arid páramos or superpáramos (Antisana, Cotopaxi, Chimborazo). Owing to its discontinuous distribution in three of the most xeric páramos of the Pichincha-Chimborazo area, this species is likely to be a relict testifying to past cold and dry periods of the last glaciation, from 25 000 to 15 000 BP, when the Ecuadorian Andes were covered by a puna-like landscape down to 3000 m (Colinvaux *et al.* 1997). Taking these data into account, we suggest that the desert-like páramo of the “arenal” has a long history and is not the result of recent anthropogenic disturbances.

Diversity in the superpáramo

The lower superpáramo (4100–4400 m) is well defined by its faunistic composition. In some of the best sampled transects (Cayambe, Pichincha, East Chimborazo, Ayapungu), this belt proves to be a zone of high biodiversity, especially regarding stenotopic elements. Similar patterns have been highlighted by recent floristic analyses (Sklenár & Balslev 2005; Sklenár 2006). Interestingly, rates of species turnover from grass páramo to lower superpáramo are quite different in humid and dry páramos, i.e. in Group 1 (Western Cordillera + Cotopaxi) and in Group 2 (Eastern Cordillera + East Chimborazo). In Group 1, a sharp threshold in species composition occurs at around 4100 m, which corresponds to the transition between grass páramo and superpáramo. In Group 2, situations are more diverse: in some cases the same species that dominate in the superpáramo are present in the upper belt of the grass páramo (Guamaní), in others there is an important turnover at around 4300 m (Cayambe, Ayapungu). These differences seem to be due to local environmental conditions, especially climatic and hydric factors.

Our data set suggests a positive correlation between humid microclimate and species richness, as illustrated by the most diverse superpáramos of Group 2

(Guamaní, Llanganatis, Ayapungu), which are also the most humid (tables 2 and 3). The number of microendemic species is also very high in these humid superpáramos. These hotspots of diversity correspond to the upper atmospheric condensation level, situated between 4000 and 4300 m in Colombia and Northern Ecuador (Van der Hammen & Cleef 1986: 158; Sklenár 2006). Higher species richness in humid oriental superpáramos is partly due to the presence of specialised riparian hygrophile species that live in streamlets or swampy areas. Such humid biotopes do not exist at the same elevation in drier páramos of the Western Cordillera.

The presence of microendemic species is significantly high in the lower superpáramo of two of the few metamorphic mountains that exist in Ecuador, Llanganatis and Ayapungu (fig. 4). But as it has been stated by Sklenár & Balslev (2005), the significance of this geologic factor for the species distributions remains dubious, whereas humidity probably plays a greater role, insofar as these páramos, along with Guamaní, receive the highest amounts of precipitation among the studied sites.

Endemism and faunistic similarity

As stated in a previous work (Moret 2005), the distribution of páramo Carabids supports the definition of areas of endemism on different scales (fig. 1). The endemicity rates that have been registered among flightless Andean Carabids is far higher than in the flora of the páramo (Sklenár & Jørgensen 1999), opening up prospects for a better understanding of the complex history of that ecosystem during the Pleistocene; but this is a different issue that cannot be treated in this paper.

There is still one point that is worth emphasising. The rates of microendemism and of species richness are clearly higher in the Eastern Cordillera than in the Western Cordillera. Among possible causes, climate must be one of the most important, given the existence of humid areas, appropriate to many Carabid species, in the major part of the Eastern cordillera. But it can also be noticed that the basal volcanic complex of Northern Ecuadorian Andes, Late Miocene to Early Pliocene in age, is much broader and higher in the Eastern Cordillera than in the Western Cordillera; in the latter, the mountains that range above 3500 m result from recent Quaternary volcanism (Barbieri *et al.* 1988). This means that conditions for the development and diversification of a highly specialised montane fauna existed much earlier in the Eastern Cordillera.

Finally, the two groups of mountains we defined above, based on altitudinal distribution of Carabid

species, are congruent with the two major floristic divisions of Sklenár & Balslev (2005). Their first group includes drier páramos (Chimborazo-west, Antisana-west, Iliniza, Cotopaxi, and Pichincha), due to the occurrence of *Plantago nubigena* and *Festuca vaginalis*, whereas their second group, based on the presence of *Pentacalia peruviana*, is composed of humid páramos (Cotacachi, Imbabura, Cajas, Cayambe, and Chimborazo-east).

Acknowledgements. This work would have remained incomplete without the help of many curators and entomologists who made available valuable materials: G.E. Ball and D. Shpeley (University of Alberta, Strickland Museum), Y. Bousquet (Canadian National Collections), A. Casale (Università di Sassari), R.L. Davidson (Carnegie Museum of Natural History), Th. Deuve (Muséum National d'Histoire Naturelle, Paris), K. Desender (Institut Royal des Sciences Naturelles de Belgique), P.M. Giachino (Museo Regionale di Scienze Naturali, Torino), I. Izquierdo y C. Martín (Museo Nacional de Ciencias Naturales, Madrid), A. Jasinski (Piastow), G. Onore, F. Maza and G. Zapata (Pontificia Universidad Católica del Ecuador), P. Ramsay and P. Smithers (University of Plymouth), A. Vigna Taglianti (Università di Roma), R. Sciaky (Milano), and L. Toledano (Verona).

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